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Decomposition of Litter on the Soil Surface

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I. Gross Composition and Production of Litter

Before considering the influences of environmental factors on litter breakdown, it will be useful to make some comments on the formation and composition of litter. Litter production and composition are highly variable and have been comprehensively reviewed by Bray and Gorham (1964).

Annual litter fall varies considerably from one forest type to another (see Jensen, Chapter 3). Rates, expressed as t ha^{-1} $year^{-1}$, vary from 5·5–15·3 in equatorial rainforests, to 2·9–8·1 in warm temperate forests, to 1·0–6·9 in cool temperate forests. In arctic conditions the range is 0·6–1·5. Production also varies during the year but the seasonal pattern varies throughout the world. In equatorial regions, litter fall is continuous throughout the year with most in the first 6 months. If dry seasons occur, leaf fall can increase. In the warm temperate forests of Eastern Australia, leaf fall is

again continuous with maxima in spring and early summer when temperature and precipitation rise. Maximum leaf fall in warm temperate forests of North America occurs in autumn as the temperature decreases. The most striking seasonal patterns occur in cool temperate forests, where autumnal cooling can lead to almost complete leaf fall in deciduous species. With gymnosperms the pattern is more variable. Finally it should be noted that litter production may vary from year to year. The ratio of highest to lowest annual litter fall varies from 2:7 for *Nothofagus* in New Zealand to 1:8 for *Acer saccharum* Marsh. in the Northern Hemisphere. Ratios can be higher for gymnosperms, a figure of 5:1 being obtained for *Pinus nigra* Arnold over a 12 year period.

Within litter, the proportion of the different components varies from one litter type to another (Table I). The major component is naturally leaf

TABLE I. Components of some litters
(From Bray and Gorham, 1964, see also Jensen, Chapter 3)

	Percentage of total litter				
	Leaf	Fruit	Branch	Bark	Other[a]
Pinus	60	11	12	14	<1
Pinus	62	17	←	21	→
Pinus	69	2	12	11	6
Picea	73	5	13	—	10
Picea-Betula	76	6	←	18	→
Betula	71	—	12	<1	16
Quercus	75	<1	15	9	—
Eucalyptus	60	15[b]	←	25	→

[a] Flowers, bud scales, fragments, epiphytes, insects.
[b] Including buds.

litter but other components are more variable. On average, the percentage of non-leaf material in forest litter is 30% for angiosperms and 29% for gymnosperms. Mineral material is present, the ash content of gymnosperms being 2–6% and angiosperms 8–14%. Organic material may be fractionated in various ways. Ether-soluble components range from 4 to 12% total dry wt, cold water-soluble matter from 3 to 14%, hot water-soluble from 3 to 9% and alcohol soluble from 3 to 13%. Hemicelluloses constitute from 10 to 19% total dry wt, cellulose 10–22%, lignin 5–8% and crude protein 2–15%.

II. Decomposition of Litter from Different Plants

It is clear that litter of different plants does not decompose at the same rate even under similar environmental conditions. This is undoubtedly due to differences in the structure and composition of their leaves and other parts.

Leaves of coniferous trees are generally decomposed more slowly than those of deciduous trees. It was estimated that a needle of *Pinus sylvestris* L. spent about 6 months in the L layer, 2 years in the F_1 and 7 years in the F_2 before being humified (Kendrick, 1959). Other parts of conifers are also resistant to decomposition. Extremely slow decomposition of softwood wood and bark was noted by Allison and Klein (1961), with many losing less than 7% of their carbon in the first 2 months after death. Allison and Murphy (1963) showed that most *Pinus* woods were decomposed more quickly than other softwoods, but still at much slower rates than hardwoods. The relative resistance of both leaves and the harder components of pine litter was reflected in the changing composition of litter in plantations of different ages (Ovington, 1962). As stands aged the proportion of harder structures, such as cones, in the litter layer, increased, while the contribution of the herbaceous ground flora decreased.

Certain non-coniferous plants also produce litter which decomposes slowly. In a study of *Calluna vulgaris* (L.) Hull litter, very small dry weight losses were recorded over long periods of time (Cormack and Gimingham, 1964). Decomposition rates varied between sites, with most rapid breakdown occurring on bare soil. In all situations, however, the litter was shed at a far faster rate than it was decomposed and hence it accumulated. Leaves of *Juncus squarrosus* L. spend about 3 years in the litter layers above acid peat, with a dry weight loss in the first year of 20–25% (Latter and Cragg, 1967). Petioles of *Pteridium aquilinum* (L.) Kuhn. lost 7–8% of their dry weight per year (Frankland, 1966). Formation of slowly decomposing mor litter in grasslands is associated with fibrous, shallow-rooting, acid-tolerant species such as *Agrostis* spp., *Festuca ovina* L., *Nardus stricta* L. and *Molinia caerulea* (L.) Moench (Barratt, 1966).

Litter of deciduous trees usually decomposes more rapidly but considerable variation occurs between different types. Melin (1930) included *Fraxinus americana* L. and *Betula papyrifera* Marsh. among fast decomposers and *Fagus grandifolia* Ehrh. among the slowest. Bocock and Gibert (1957) observed that leaves of *Betula verrucosa* Ehrh. and *Tilia cordata* Mill. were more rapidly decomposed than those of *Quercus robur* L. and *Q. petraea* (Mattusch.) Liebl. (Table II). Comparison of decomposition rates on different sites showed that they were faster on mull sites although the relative rates of various species were generally similar on all sites.

TABLE II. Disappearance of tree leaves placed on various sites (Data from Bocock and Gilbert, 1957)

	Loss in dry wt (%) in 6 months		
	Mull	Moder	Peat
Betula verrucosa (ex limestone)	82·9	26·3	27·8
Betula verrucosa (ex peat)	91·5	29·4	24·8
Tilia cordata	55·6	22·6	17·8
Quercus petraea	26·2	23·2	21·8
Quercus robur	17·4	17·0	16·7

Dry weight losses of leaves of *Quercus petraea* and *Fraxinus excelsior* L. in nylon nets on mull and moder sites were compared by Bocock *et al.* (1960). Rates of decomposition of *Quercus* were similar on both sites but *Fraxinus* disappeared more rapidly on the mull, only a few midribs remaining after 6 months. Figures after 6 months (expressed as % dry weight remaining) were *Fraxinus* on mull 5%, on moder 50%, *Quercus* on mull 85%, on moder 78%.

Disappearance of litter of a number of trees and shrubs in coarse mesh bags was followed by Bocock (1964). These bags allowed access to soil fauna, especially earthworms, and resulted in considerable differences in rates between mull and moder sites for some species. For example, the dry weights remaining after 148 days on the mull were about 10% for *Alnus glutinosa* (L.) Gaertn. and 20% for *Betula pendula* Roth. On moder the figures were 55% and 70% respectively (see Table XI).

Heath *et al.* (1966) studied breakdown rates of leaf discs from various plants held in different sized mesh bags. Three groups were recognized: (i) the fastest, in which microbial decomposition alone caused their disappearance (e.g. *Brassica oleracea* L., *Vicia faba* L.); (ii) fast at first but some persistence in small mesh bags (e.g. *Betula alba*, *Fraxinus excelsior*, *Ulmus campestris*); (iii) much slower in large or small mesh bags (e.g. *Quercus robur*, *Fagus sylvatica*). The effect of earthworms on disappearance of these leaves was most marked.

Differences in decomposition rates of leaves from the same plant were noted by Heath and Arnold (1966). "Shade" leaves, which were softer, disappeared more rapidly than "sun" leaves. This was attributed to the preference of worms for the softer leaves. It was also noted that hard leaves had a higher polyphenol content.

III. Environmental Factors and Decomposition

Consideration of environmental factors must include those which we may regard as "external" to the decomposition process (e.g. moisture, temperature) together with "internal" influences such as the chemical composition of leaves (see Miller, Chapter 4).

A. Temperature

This is undoubtedly one of the major factors controlling litter decomposition. Rate of decomposition in a tropical rainforest was found to be 8·2 t ha^{-1} $year^{-1}$ (Wanner, 1970), while in arctic litter containing lichens, *Luzula confusa* and *Poa arctica*, a rate of less than 1·2 t ha^{-1} $year^{-1}$ was estimated (Douglas and Tedrow, 1959). To a large extent such results are explained by differences in air temperatures and moisture supply. Results of various work on tropical and temperate forests were summarized by Madge (1965) (Table III). In tropical forests there is generally little or no litter accumulation with a fast turnover of organic matter in the soil. In temperate forests, little accumulates, this being particularly marked in coniferous stands. It was not possible, however, to show a clear relationship between leaf fall, litter accumulation, temperature and rainfall.

In the upper layers of soil, steep temperature gradients exist (Macfadyen, 1968). The temperature at the surface is often clearly related to air temperature, especially if the surface is shaded, and litter acts as an insulating layer on the soil. Travleev (1960) measured temperatures throughout the year in the air, in the litter and at a depth of 10 cm in the soil (Table IV). It is clear that litter temperatures were close to those of air, generally being a little lower. These average temperatures disguise the considerable short term and spatial variations which occur.

It is not surprising, therefore, that correlations have been found between rates of litter decomposition and air temperatures measured on a local or wide scale. Seasonal changes in temperature have been related to decomposition rates. Rates of carbon dioxide evolution from *Quercus alba* and *Pinus rigida* Mill. forests were assessed by measuring carbon dioxide accumulation at night during temperature inversions (Woodwell and Dykeman, 1966). Spring and summer rates were 2–3 times greater than those in winter. Seasonal temperature effects on mull and mor litter breakdown were noted by Witkamp and van der Drift (1961). Different temperatures at various altitudes result in different decomposition rates. Thus losses in weight of *Sphagnum* litter were greater in lowland than upland bogs, the temperature differences being about 10°C throughout the year (Clymo, 1965).

TABLE III. Litter fall and accumulation in various forests
(Data from Madge, 1965)

Vegetation	Rainfall (cm year^{-1})	Temperature (°C average year^{-1})	Litter fall (kg ha^{-1} year^{-1})	Litter accumulation (kg ha^{-1})	Ratio fall/ accumulation	Authors
Tropical regions:						
Broad-leaved rainforest	825	25·5	7560	4500	1·7:1	Jenny (1948) Jenny *et al.* (1949)
Broad-leaved forest	255	21	9000	14,700	1:1·6	Jenny (1948) Jenny *et al.* (1949)
Mixed rain forest	170	24·5	12,300	4300	2·9:1	Bernard (1945) Laudelout and Meyer (1954)
Moist semi-deciduous-moist evergreen forest	163	18	9400	2220	4·2:1	Nye (1961) Greenland and Kowal (1960)
Mixed dry lowland forest	120	27	5600	1700–2450	2·2:1	Madge (1965)
Temperate regions:						
Quercus woodland	75	10	1380	39,980	1:29	Jenny *et al.* (1949)
Pinus stand	75	10	2800	167,700	1:59·6	Jenny *et al.* (1949)
Mixed woodland	85	10	3100	3600	1:1·2	Witkamp and van der Drift (1961)

TABLE IV. Average temperatures in air, litter and soil (°C)
(From Travleev, 1960)

	September–November	December–February	March–June
Quercus			
Air	7·7	−1·5	10·0
Litter surface	9·0	−1·2	13·8
Beneath litter	6·2	0·8	6·8
Soil 10 cm depth	4·9	0·2	5·3
Fraxinus			
Air	10·2	−1·4	13·2
Litter surface	10·5	−1·2	20·0
Beneath litter	10·5	−1·0	16·6
Soil 10 cm depth	8·5	−1·0	14·0

Correlations of temperature with microbial respiration and carbon dioxide evolution from litter of *Pinus echinata* Mill., *Quercus alba* L. and *Acer rubrum* L. have been obtained (Witkamp, 1966*a*, *b*). A daily cycle of carbon dioxide evolution with a pre-dawn minimum and an afternoon maximum. This is correlated with the daily temperature cycle at the litter surface (Witkamp, 1969*a*; Witkamp and Frank, 1969). When the soil temperature exceeds that at the surface, thermal convection of carbon dioxide-rich air may occur. Temperature also influences mineral cycling in litter (Witkamp, 1969*b*). The influence of temperature on decomposition processes in grass litter in the laboratory was studied by Floate (1970*b*). Over the experimental period, litter lost 40% of its carbon at 30°C and 12% at 5°C. Similarly 5·4% of its nitrogen was mineralized at 30°C and −0·3% at 5°C.

Bleak (1970) showed that litter decomposition could occur under snow. When the snow depth was more than 60 cm temperatures at the soil surface ranged from −2·5 to +1·2°C. Loss in weight of grass and broad-leaved litter occurred, figures ranging from 30% for *Agropyron trachycaulum* (Link) Malte ex H. F. Lewis to 51% for *Mertensia asironica* var. *leonardi* (Rydb.) I. M. Johnst., losses given are averages of losses through two consecutive winter periods (October–June).

Forest fires also cause major changes in the temperature of the litter and the surface soil, changes in the latter being less marked. Hoffman (1924) found that surface temperatures of 850°C resulted in organic matter at 0·75 in. depth reaching 49°C, while at 1·5 in. it was only 16°C. Increasing moisture content of soil resulted in better heat penetration. Although these

changes are not permanent, some less temporary effects occur. Thus, the blackened, charred areas show greater fluctuations in temperature than unburned areas (Phillips, 1930).

B. Moisture and Aeration

Relatively little attention has been paid to the moisture characteristics of litter as compared with soil. Most measurements have been expressed as percentage moisture content or percentage moisture holding capacity, rather than moisture tension.

The water-holding capacity of litter can affect soil erosion, rate of water infiltration to roots and the likelihood of forest fires (Kittredge, 1955). It was found that the field moisture capacity varied with litter type, ranging from about 150% wt water/wt dry soil (litter) in *Picea menziesii* (Mirb.) Franco (douglas fir) to 206% for *Pinus attenuata* (knobcone pine). Grass litter had a much higher capacity of 245%. Clary and Ffolliott (1969) found that the moisture holding capacity of litter varied with depth, with greatest capacities being in the amorphous H layers and lowest in the L layers. Thus when water was added, 85% was retained by the H layer and only 3·5% by the L layer. Although little attention has been given to humidity of air in litter, this will also increase in the lower layers and influence the activity of decomposers. The importance of relative humidity on fungal colonization of *Dactylis glomerata* L. (cocksfoot) culms was demonstrated by Webster and Dix (1960).

The influence of moisture on litter breakdown has been demonstrated by a number of workers. In periods of drought, decomposition of mull and mor litter was retarded and numbers of saprophagous animals in litter

TABLE V. Approximate densities per m^2 of some saprophagous groups in litter from mixed hardwood coppice on sandy soil before and after a dry summer (1959). (From van der Drift, 1963.)

	Mull		Mor	
	1957	1961	1957	1961
Lumbricidae	100	50	60	40
Pulmonata	20	30	5	—
Isopoda	40	10	20	5
Diplopoda	100	40	35	10
Tipulidae	80	30	5	5
Enoicyla	900	—	—	—

were reduced (van der Drift, 1963) (Table V). Interaction of temperature and moisture in controlling mull and mor decomposition was noted by Witkamp and van der Drift (1961). In arctic conditions, moisture and

temperature were important factors influencing carbon dioxide evolution in the field (Douglas and Tedrow, 1959). Weight losses of *Quercus alba*, *Fagus grandifolia* and *Morus rubra* L. litters were correlated with moisture content (Witkamp, 1963). A correlation with carbon dioxide evolution in the field from litter of *Pinus echinata*, *Quercus alba* and *Acer rubrum* was also obtained (Witkamp, 1966*b*). Microbial respiration in litter bags was influenced in decreasing order by temperature, bacterial density, moisture, and age of litter (Witkamp, 1966*a*). In a laboratory study, Floate (1970*c*) found that moisture content changes had only minor effects on mineralization of *Nardus* and *Agrostis–Festuca* litter.

Aeration of much litter is obviously directly associated with moisture content. The most limiting effects on decomposition occur when litter is waterlogged, resulting in impaired gaseous diffusion and development of anaerobic conditions. This may not be a common situation in terrestrial litter.

Little information is available on gas concentrations in litter or their influence on decomposition. Brierley (1955) analysed gas in tubes placed at the junction of the humus and litter layers in a *Fagus* forest. Results showed fluctuations in oxygen content in litter from 19·5 to 20·6% (cf. 20·9% for above-ground air). The carbon dioxide content varied from 0·1 to 0·7% (cf. 0·03% for above-ground air). No correlations with depth were found. Thus the gaseous content of litter is probably often close to that of the air above it.

C. pH and Base Content

The reaction and base content of litter are very variable and depend on such factors as the leaf types in the litter, the base status of the underlying soil and the extent to which the litter has been decomposed.

Most decomposing leaf litter is acidic, with that from conifers being more acidic than that from hardwood deciduous trees. Therefore in mixed forests, hardwood litter tends to increase the base content, improve the buffering capacity and decrease the acidity. Plice (1934) studied litter from a wide range of North American trees and distinguished between hypobasic, middle and superantacid types (Table VI). These groups were distinguished by their calcium oxide content (3·6–5·7%, 2·2–3·1%, 0·3–2·1%, respectively), their antacid buffering capacity (3·5–3·98, 3·0–3·4, 1·5–2·9 mequiv. hydrogen ions inactivated by 5 g dry wt litter) and their acidity (pH 3·3–4·0, 4·1–4·5, 4·6–5·9). Only a few litter types had a pH above 4·5 (e.g. *Ulmus americana* L., *Acer platanoides* L., *Fraxinus americana*) and these had a high base content. However, the base content of some of the more acid litters was also high (e.g. *Acer saccharum*). Lutz and Chandler (1946) recognized three groups of leaves on the basis of their

TABLE VI. Base content, buffering capacity and reaction of leaf litters (From Plice, 1934)

Hyberbasic series	Middle series	Super-antacid series
1. High bases and buffer, acidity medium. *Carya microcarpa* Gray	1. High bases and buffer, acidity weak. *Carya glabra* (Mill.) Sweet *Magnolia acuminata* L. *Thuya occidentalis* L.	1. Medium bases, high buffer, acidity weak. *Acer platanoides* *Ulmus americana*
2. Medium bases, low buffer, acidity strong. *Picea canadensis* Gray, B. & B. *Picea excelsa* Link	2. Medium bases and buffer, acidity weak. *Fraxinus americana* *Betula lutea* Michx. f. Acidity strong. *Acer saccharum*	2. Low bases, medium buffer, acidity medium. *Castanea dentata* (Marsh.) Borkh. *Quercus rubra* L. sec. Duroi *Acer rubrum* *Quercus alba* *Larix europea* DC. *Larix laricina* (Duroi) K. Koch
3. Fairly low bases, low buffer, acidity strong to extreme. *Abies balsamea* (L.) Mill. *Picea maritima* *Pinus banksiana* Lamb *Tsuga canadensis* (L.) Carr	3. Fairly low bases and buffer, acidity weak. *Fagus grandifolia* Acidity strong. *Quercus Prinus* *Pinus sylvestris* *Pinus rigida* *Pinus strobus* L. *Pinus resinosa* Ait.	

calcium content, those with >2% calcium (% dry wt) (e.g. *Populus tremuloides* Michx.), those with 1–2% (e.g. *Picea abies* (L.) Karst.) and those with >1% (e.g. *Pinus sylvestris*).

Ovington and Madgwick (1957) found a broad correlation between pH of the soil and that of tree leaves and litter. This was most noticeable with hardwoods. Acid soil had litter of similar reaction but alkaline soil had litter with a pH lower than that of the soil. The F and H layers were more acidic than the L layers in 68 out of 73 conifer plantations studied. In hardwood litters there were no consistent differences between the layers.

The extent of decomposition of leaves also affects their reaction. Quite large changes occur during the initial phases of decomposition. Sjörs (1959) showed that most litters became less acidic during the first 34 days of decomposition on soil (Table VII). The initial decrease in acidity was

TABLE VII. Changes in litter reaction (pH) during early stages of decomposition (From Sjörs, 1959)

	Days on soil				
	0	5	12	21	34
Acer platanoides	5·3	4·8	4·7	4·8	5·0
Betula verrucosa	5·3	5·5	5·8	5·7	6·3
Alnus incana (L.) Moench	5·9	6·2	6·2	6·0	—
Populus tremula L.	5·6	5·8	6·3	6·5	6·8
Sorbus intermedia (Ehrh.) Pers.	4·8	5·8	6·1	6·1	6·4
Sorbus aucuparia L.	5·4	6·7	6·4	6·7	6·7
Fagus sylvatica L.	5·8	6·3	6·3	5·8	6·1
Ulmus glabra Huds.	5·9	5·8	5·9	5·9	6·4
Corylus avellana L.	6·2	6·9	6·7	6·5	6·5
Salix caprea L.	6·4	6·7	6·7	6·5	7·1
Fraxinus excelsior	6·3	7·6	7·4	6·9	7·3
Calamagrostis epigeios (L.) Roth.	5·8	5·9	5·6	5·7	6·2

almost certainly due to leaching of acidic solutes (e.g. organic acids) in the cell sap. Nykvist (1959*a*, *b*) showed clearly that material leached from litter became less acidic with time. The extent of the rise in pH depended on the aeration of the litter, the length of the leaching period and the susceptibility of the litter to decomposition. Thus in aerobic conditions, the pH of *Fraxinus* leachates rose from 5·6 to 7·6 in 24 h, and to 7·1 in 42 days. In anaerobic conditions, the corresponding values were 5·5 and 5·4. Similar, though less clear-cut, results were obtained with *Pinus* litter. Initial rises in pH were also found by Mattson and Koutler-Anderson (1954), the greatest rises occurring in litters with a high initial excess base content. However, after a few years a decrease in pH occurs as bases are removed and humic acid forms. After 14 years, humus from all the litters, with the exception of *Ulmus*, was acidic.

Base content of litter also varies throughout the year. Wright (1956) observed a marked fall in the content of calcium, potassium, sodium and magnesium in *Pinus* litter in summer. Remezov (1961) examined the effects

of leaching on *Quercus* litter. The percentages remaining after 2 months were—

	K	P	N	Mg	Ca	Si	Al	Fe
%	46	53	65	65	72	83	90	100

Losses of potassium from the F layer were most marked. Latter and Cragg (1967) studying *Juncus* litter found more than 50% loss of all inorganic ions tested within 5 months, with potassium, phosphorus, magnesium and calcium losses being most marked. A complicating factor is the carriage of substances into the litter from the canopy by precipitation. Carlisle *et al.* (1966) showed that of the total amounts present in *Quercus* litter, 72% of the potassium came from the canopy.

There is evidence that the rate of litter decomposition is correlated with its base content. It is well known that many potential decomposer organisms are inactive or less active when the pH is much below 5·0. The excess base contents of freshly fallen leaves were measured by Broadfoot and Pierre (1939) and three groups were recognized, the extent of decomposition in the first 6 months increasing with base content (Table VIII). A marked

TABLE VIII. Excess base content of some tree leaves
(From Broadfoot and Pierre, 1939)

	Species	Excess base content	% decomposition in 6 months
Group 1	*Pinus strobus*	42	17
<75 mequiv excess base	*Pinus rigida*	44	21
per 100 g	*Fagus grandifolia*	70	17
	Platanus occidentalis L.	72	21
Group 2	*Quercus alba*	80	28
75–110 mequiv excess base	*Quercus velutina* Lam.	88	29
per 100 g	*Juniperus virginiana* L.	99	40
	Acer saccharum	109	33
Group 3	*Liriodendron tulipifera* L.	121	55
>110 mequiv excess base	*Robinia pseudo-acacia*	145	47
per 100 g	*Cornus florida* L.	152	43
	Aesculus hippocastanum L.	174	30

positive correlation was obtained for the last 4 months of the decomposition period (Table IX). Voigt (1965) did not obtain a clear correlation between leaf calcium content and weight or nitrogen loss but greatest nitrogen losses occurred in species with the highest calcium content (Table X). Addition of calcium carbonate also stimulated nitrogen loss (see p. 624).

TABLE IX. Relative effects of independent variables on litter decomposition (calculated from standard partial regression coefficients and expressed as percentage). (From Broadfoot and Pierre, 1939)

	0–2 months	2–6 months	0–6 months
% excess base	4	97	19
% water soluble organic matter	51	1	44
% total nitrogen	45	2	37

D. Water-soluble Organic Matter Content

This component of the litter provides a readily available energy source for decomposers and has, therefore, most influence in the initial stages of decomposition. Usually there is a rapid loss of soluble organic matter due to microbial utilization and leaching. A 50% decrease in the first 3 months was recorded for *Casuarina* litter (Burges, 1958). Sowden and Ivarson (1962) found that sugars were removed more rapidly from deciduous than from coniferous litter during the first 165 days. Broadfoot and Pierre (1939) noted a correlation between litter decomposition and the content of soluble organic matter. This was most marked during the first 2 months (Table IX). Melin (1930) suggested that water-soluble material only influenced decomposition rates for the first few weeks. The content of hot-water-soluble materials in *Fraxinus excelsior* leaves was 32% (w/w), while in *Quercus petraea* it was only 18% (Gilbert and Bocock, 1960). After a month the content of the *Fraxinus* dropped to 1·5% but in the *Quercus* the decline was more gradual.

Although it seems that amounts of these simpler carbon compounds decrease rapidly in the early stages of decomposition, they are not completely mineralized. When ^{14}C-labelled glucose was added to soil, 11% of the carbon was still present in soil after 30 days incubation in the laboratory (Mayaudon and Simonart, 1959). Such compounds may in part be resynthesized into microbial tissues or products more resistant to decay than the original (Clark and Paul, 1970). There is also evidence that microbial

TABLE X. Decomposition of litter incubated under laboratory conditions for three months at 32°C. (From Voigt, 1965)

Species	Ca in fresh litter (%)	N in fresh litter (%)	Litter alone			Litter + $CaCO_3$		
			Wt loss (%)	N deficit (%)	Final pH	Wt loss (%)	N deficit (%)	Final pH
Alnus rugosa (Du Roi) Spreng.	1·15	2·18	34·2	24·3	5·5	33·6	41·7	7·0
Liriodendron tulipifera	2·16	1·87	48·8	36·8	7·1	47·9	53·1	8·1
Cornus florida	2·20	1·63	44·6	17·8	7·2	33·4	23·1	7·4
Tsuga canadensis	0·39	1·65	36·8	12·9	6·3	23·4	11·9	6·8
Pinus resinosa	0·36	1·50	18·2	12·7	5·7	17·8	11·4	6·6
Juniperus virginiana	1·30	1·40	31·5	13·1	7·3	32·8	14·5	8·2
Hardwoods (mean)	1·84	1·89	42·5	26·3	6·5	38·3	39·3	7·2
Conifers (mean)	0·68	1·52	28·8	12·9	5·9	24·7	12·6	7·1

utilization of compounds such as glucose and lysine is inhibited by tannins which are present in litter (Basaraba, 1966; Benoit *et al.*, 1968).

E. Nitrogen Content

During decomposition, carbon is used as an energy source by decomposers while nitrogen is assimilated into cell proteins and other compounds. Thus a high nitrogen content in the original material promotes decomposition, at least in the early stages. Fresh plant materials vary considerably in their nitrogen content. Woody materials have from about 0·2–0·5% (w/w) while herbaceous plants such as grasses have from 0·5–1·5% and legumes have 1·5–3·0% (Bartholomew, 1965). Tropical forest litter has a higher nitrogen content than that of temperate forests (Nye, 1961). In the early stages of decomposition, residues with low nitrogen contents may show an increase in organic nitrogen as available nitrogen is used by initial colonizers. On the other hand, those with more nitrogen show a decline in organic nitrogen as net mineralization occurs (Bartholomew, 1965). After the initial period of breakdown, further net changes in organic nitrogen are slow and some remains throughout the decomposition process.

The significance of initial nitrogen contents to decomposition of litter has received some study (see Forbes, Chapter 23; Gray and Biddlestone, Chapter 24). Nitrogen content of deciduous leaves is somewhat higher than that of conifers. Alway *et al.* (1933) found that there was 1·5 times as much nitrogen in litter of *Acer saccharum* and *Tilia glabra* Ventenat as in that of *Pinus* spp. Nitrogen contents of a range of litters were determined by Broadfoot and Pierre (1939), figures ranging from 0·46% (w/w) for *Pinus rigida* to 2·06% for *Robinia pseudo-acacia* L. Correlation between rate of decomposition and nitrogen content was greatest during the first 2 months (Table IX). Fenton (1958) obtained figures of 1·58% for *Betula* compared with 0·62% for *Pinus radiata* Don, while Ivarson and Sowden (1959) recorded 0·79% in conifer litter and 1·01% for deciduous litter. Average values for hardwood leaves were slightly greater than those of conifers (Voigt, 1965) (Table X). Nitrogen contents of a wide range of leaves were determined by Bocock (1964); generally litter richer in nitrogen decomposed more rapidly and rates on mull were faster than on moder. The nitrogen content of slowly decomposing *Nardus* litter was 0·89% (w/w) for *Agrostis–Festuca* litter it was 1·39% (Floate, 1970*a*).

Changes in nitrogen compounds during decomposition depend to some extent on the initial nitrogen content. Little overall change in nitrogen content occurs during decomposition of some leaves. After 2 years, 85·9% of the original nitrogen remained in *Pinus sylvestris* litter and 95·9% in

Betula (Mikola, 1955). Some of this nitrogen was undoubtedly in microbial cells. Little change occurred in *Abies*, *Pinus* and *Picea* litter (Hayes, 1965). When litter in nylon nets was placed on different sites, the nitrogen content of *Fraxinus excelsior* was constant for the first 7 months on mull but increased on moder (Gilbert and Bocock, 1960). Increases in *Quercus petraea* on moder were considerable, reaching 160% in 10 months. In a

TABLE XI. Nitrogen contents of freshly fallen leaves of various trees and their decomposition. (From Bocock, 1964)

Species	Nitrogen (% dry wt)	Percentage of initial nitrogen left after 148 days[a]	
		on Mull	on Moder
Alnus glutinosa	3·06	10	55
Acer pseudoplatanus	2·52	20	50
Fraxinus excelsior	1·55	25	45
Tilia cordata	1·45	40	80
Corylus avellana	1·39	73	76
Salix sp.	1·38	45	60
Ulmus glabra	1·32	20	15
Fagus sylvatica	1·17	65[b]	80
Betula pubescens Ehrh.	1·13	42	75
Betula pendula	1·07	20	70
Aesculus hippocastanum	0·89	75	70
Quercus robur	0·79	40[b]	60
Quercus petraea	0·77	50[b]	65
Castanea sativa Mill.	0·69	75	70

[a] Approximate values from figures.
[b] After 267 days.

later study (Bocock, 1963) it was shown that nitrogen was added to the oak litter by atmospheric precipitation, insect frass and plant material falling from the canopy. Up to 25% of the inorganic nitrogen in rain was taken up by the litter. In a study of several litters, Bocock (1964) observed that the percentage nitrogen content of most increased during decomposition, with greater increases occurring on moder than on mull sites. Such additions of nitrogen have been overlooked in many previous studies of changes in nitrogen levels in litter.

Recovery of nitrogen from decomposing litter was measured by Voigt (1965). Weight losses and nitrogen deficits were more marked in hardwoods

than conifers. Loss of nitrogen was sometimes increased by adding calcium carbonate and in most cases greatest nitrogen deficits were associated with relatively high pH values (Table X).

In a laboratory study of nitrogen mineralization in soil, Fenton (1958) found that additions of litter produced a marked decrease in mineralization. The depression produced by *Pinus radiata* litter was greater than that by *Betula* sp. Release of nitrate occurred with the latter but not with *Pinus*. Ivarson and Sowden (1959) noted that the initial release of ammonia was greater from deciduous than from coniferous litter. Nitrate formation occurred in the former but not the latter and they suggested that this was due to the higher initial nitrogen content in the deciduous litter. The amount of nitrogen mineralized during decomposition of grassland litters can also be related to their initial nitrogen contents (Shaw, 1958; Floate, 1970*a*). In *Agrostis–Festuca* litter, 13·9% of the original nitrogen (1·39% w/w) was mineralized compared with 6·8% from *Nardus* (0·89% w/w) during the same period (Floate, 1970*a*).

Non-leaf materials in litter, such as twigs and bark, have a lower nitrogen content than that of leaves. Partially decayed wood persists for many years and comprised from 14 to 30% (w/w) of the litters in North American forests (McFee and Stone, 1966). Nitrogen in wood and bark of trees was determined by Allison and Klein (1961), and Allison and Murphy (1962, 1963) (Table XII). The effect of nitrogen on decomposition was

TABLE XII. Nitrogen content of bark and woods
(From Allison and Klein, 1961; Allison and Murphy, 1962, 1963)

	% nitrogen	
	Wood	Bark
Softwoods	0·051–0·227	0·038–0·390
Pines	0·038–0·130	0·048–0·179
Hardwoods	0·057–0·104	0·102–0·413

also studied. With hardwoods, a significant increase in oxidation of wood carbon resulted from additions of nitrogen; for pines, increases were much smaller (Table XIII). No effects on decomposition of bark were obtained. Allison and Klein (1961) showed that decomposition of most softwoods was so slow that the soil nitrogen supply was adequate and additions of nitrogen gave no increases in decomposition rates.

Thus the initial nitrogen content of litter can have many influences on its subsequent decomposition. Effects are most marked in earlier stages of

decomposition of litters with a high nitrogen content. In later stages there is little net change and organic nitrogen becomes more resistant to decomposition. This is possibly due to the synthesis of more recalcitrant nitrogenous organic compounds by decomposers and the protective association of proteins with polyphenols.

TABLE XIII. Decomposition of wood and bark with and without addition of nitrogen (From Allison and Murphy, 1962, 1963)

	% C oxidized after 60 days (average values)			
	Wood		Bark	
	−Nitrogen	+Nitrogen	−Nitrogen	+Nitrogen
Hardwoods	30·3	45·1	22·4	24·5
Pines	16·2	16·9	8·7	8·6

F. Polyphenol Content

Plants contain a variety of polyhydroxy phenols which comprise from 5 to 15% of their dry weight. Some may be extracted with water to give tannins and they may be thus leached from litters into the soil. There is increasing amount of evidence for the importance of these substances in controlling rates of litter decomposition. After initial loss of various components, decomposition rates decrease and organic matter becomes more resistant to attack. Minderman (1968) found that decomposition of litter in the field did not equal the sum of the decay rates of its individual components. Clark and Paul (1970) showed that this could be overcome by correcting data for individual components to allow for resynthesis of secondary metabolites which were more resistant. The accumulation of condensed or polymerized polyphenols with very slow decomposition rates is an important phenomenon. These may originate from the litter itself or be synthesized by microbes. Minderman pointed out that after 10 years or more, the rates of accumulation of litter are primarily determined by such components.

The role of polyphenols in the formation of different litter types has been studied (see Lofty, Chapter 14; Harding and Stuttard, Chapter 15; Edwards, Chapter 16). Handley (1954) showed that fresh leaves of some plants contained soluble substances which resembled tannins and caused precipitation of proteins. Later he obtained complexes of protein with these extracts and determined their stability by measuring uptake of

nitrogen released from them using seedlings (Handley, 1961). Resistance was most marked in complexes prepared with leaf extracts of the mor-forming *Calluna vulgaris*. Those made with *Circaea lutetiana* L. promoted seedling growth by giving a controlled release of nitrogen. It was therefore suggested these protein-precipitating substances were of fundamental importance in determining the type of litter formed.

More extractable tannins occurred in surface litter at mor than at mull sites (Coulson *et al.*, 1960). There was also a greater quantity and diversity of polyphenols in fresh, senescent and recently fallen leaves of the same plant when grown on nutrient-poor mor than on nutrient-rich mull sites. Thus an interrelationship of soil, leaf composition and litter decomposition was indicated. Davies *et al.* (1964*b*) showed that in sand cultures, shortage of nitrogen and phosphorus increased amounts of polyphenols in leaves. Extracted polyphenols have been shown to form complexes with a variety of substances. Gelatin was tanned and its stability was greatest when tanning occurred at pH 3·0–5·0 (Davies *et al.*, 1964*a*). Similar results were

TABLE XIV. Influence of tannins[a] on decomposition of various substrates

Substrate	% inhibition		Authors
	pH 4·0	pH 7·0	
Gelatin	51	30	
Gliadin	54	21	Basaraba and Starkey (1966)
Peptone	32	38	
Glucuronic acid	6	−2	
Polygalacturonic acid	30	12	
Pectin	16	25	Benoit and Starkey (1968*a*)
Hemicellulose	62	59	Starkey (1968*a*)
Cellulose	35	51	
Young *Secale* plants	53	50	Benoit *et al.* (1968)
Mature *Secale* plants	47	48	
Chitin	33[b]	—	
Saponin	39[b]	—	Lewis and Starkey (1968)
Starch	49[b]	—	
Pectin	25[b]	—	

[a] Various tannins at 2% (w/w).
[b] 1·0% tannin in soil at pH 4·2.

obtained by Basaraba and Starkey (1966) who combined tannins with gelatin and gliadin at two different pH levels. Thus complexes formed in acidic litter are likely to be more resistant. Inhibitory effects on decomposition of a number of other substances have been shown (Table XIV). Resistance is probably conferred by inhibition of microbial enzyme action and the increased recalcitrance of the complex, those formed by high molecular weight tannins being the most stable (Benoit and Starkey, 1968*b*). Thus there is good evidence for the importance of polyphenols in determining differential rates of litter decomposition, their effects being influenced by the pH of the litter and the soil nutrient status.

In the later stages of decomposition, humic materials, which also contain polyphenols, can influence decomposition. It has been shown that the action of microbial proteolytic enzymes can be inhibited or stimulated by humic acids (Ladd and Butler, 1969).

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